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Gametogenesis and Reproductive Cycle of the Surf Clam *Mesodesma donacium* (Lamarck, 1818) (Bivalvia: Mesodesmatidae) at Queule Beach, Southern Chile

by

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Abstract. The gonadal organization, cytological characteristics of gametogenesis, and reproductive cycle in the surf clam *Mesodesma donacium,* from Queule Beach, southern Chile, were studied histologically using light microscopy. Monthly analysis of the proportion of sexes revealed a sex ratio of 1:1. In both sexes, gonads are ramified organs bearing numerous follicles closely packed among coils of the intestine. Gametogenesis follows the general plan described in most marine bivalves. Gametes at different stages of maturation can be recognized by their shape, size, and nuclear features in both sexes. The reproductive cycle is annual, with a maturation period from June through November (winter and spring). Spawning extends from December to April (summer and early autumn), peaking in December and January. Gonads undergo a short recovery period during May and then start a new cycle.

INTRODUCTION

The reproductive cycles of mollusks of commercial value inhabiting Chile's extensive coastline have been described from a variety of locations on the coast. Among the lamellibranch bivalves are *Aulacomya ater* (LOZADA, 1968; SOLÍS & LOZADA, 1971), *Choromytilus chorus* (LOZADA *et al.,* 1971; PEREZ-OLEA, 1981), *Ostrea chilensis* (WALNE, 1963; SOLÍS, 1967) and *Venus antiqua* (LOZADA & BUSTOS, 1984). These studies, in addition to furnishing reproductive data that have allowed an adequate management of these species, have also shown variations in the timing of gametogenesis and spawning in populations from different geographical areas. These latitudinal variations are ascribed to environmental factors that present local variations and exert exogenous control on reproduction. Among these factors, the most relevant are temperature and abundance of food (GIESE & PEARSE, 1977).

The reproductive cycle of the surf clam *Mesodesma donacium* has been studied by BROWN & GUERRA (1979) in Guanaqueros (30°15′S, 71°41′W) and TARIFEÑO (1980) at the Laguna Beach area of Valparaíso (32°30′S, 71°30′W). These studies have shown differences in the timing of gametogenesis and spawning period in the populations studied. The present study describes the sex ratio, gametogenesis, and seasonal gonadal changes of a surf clam population from Queule Beach (39°25′S, 73°13′W). This locality was selected as the study area because it has potential for commercial operations and the area appears to contain a large population of the surf clam.

MATERIALS AND METHODS

Monthly samples of surf clams were collected from a bed in the mid-littoral level of Queule Beach (39°25′S, 73°13′W) from August 1983 to November 1984. Each sample consisted of 230 clams. From these samples, 15 males and 15 females in the shell length range of 61 to 75 mm were selected for histological study. This size range was chosen to avoid inclusion of juvenile surf clams (sexually immature individuals). The viscera were fixed in aqueous Bouin's fixative. After embedding in paraffin, 7-μm serial sections were cut and stained with hematoxylin and eosin. Ten to 15 sections through different regions of the gonads of each specimen were examined under the light microscope to determine the gonadal organization, the cytological characteristics of gametogenesis, and the seasonal gametogenic cycle.

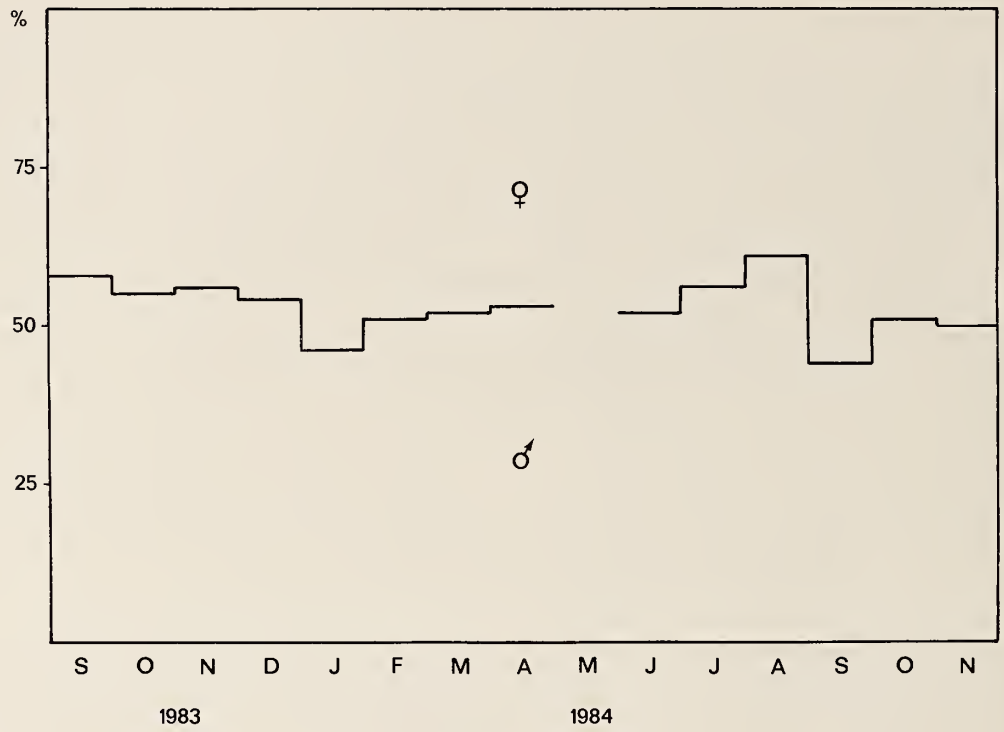

Figure 1

Proportions of females and males in the *Mesodesma donacium* population from Queule Beach.

The remaining specimens of the monthly samples were used to determine the sex ratio and the dry weight of the soft tissues. Chi-square analysis was used for sex-ratio determinations. To determine the dry weight, the body soft tissues were kept in an oven at 90°C until reaching constant weight.

Water temperature data during the study period were supplied by the Marine Station at Mehuín of the Zoological Institute, Universidad Austral de Chile.

RESULTS

Mesodesma donacium is a dioecious species as revealed by microscopic examinations. These results support former reports of studies on populations of this species occurring at different locations on the Chilean coast (Brown & Guerra, 1979; Tarifeño, 1980). Monthly analysis of the proportion of sexes in the mature population of *M. donacium* revealed a sex ratio of 1:1. Of the total number examined, 52% of the individuals were males, 46% females, and 2.1% indeterminate (Figure 1). Sexual dimorphism is absent.

Male Gonad and Germ Cells

The male gonad consists of numerous follicles located in the visceral mass surrounding the intestinal coils. The follicles vary in shape and size and are delimited by a thin, cellular, enveloping membrane (Ancel's layer) (Figure 2). Fibroblast-like cells with spindle-shaped nuclei are seen in the follicle walls (Figures 3, 4). The cytoplasm of these cells is difficult to visualize.

In the period of maximum gonadal activity, the follicles are crowded with cells at different stages of spermatogenesis. The cells of particular stages can be recognized by their nuclear features (shape, size, and staining properties) and by their location in the gonadal follicles (Figure 5).

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Explanation of Figures 2 to 7

Figure 2. Topographical view of the male gonad of *Mesodesma donacium*. The well delimited follicles (F) show diversity in size and shape and occupy the visceral mass (mesosoma) surrounding the intestine (I). ×20.

Figure 3. Primary spermatogonia (spg1) and secondary spermatogonia (spg2) lying in the periphery of the follicle. Close to the spermatogonia, the nucleus of a supporting cell (sc) can be seen. The spindle-shaped nucleus (arrow) is from a cell of the follicle wall. ×500.

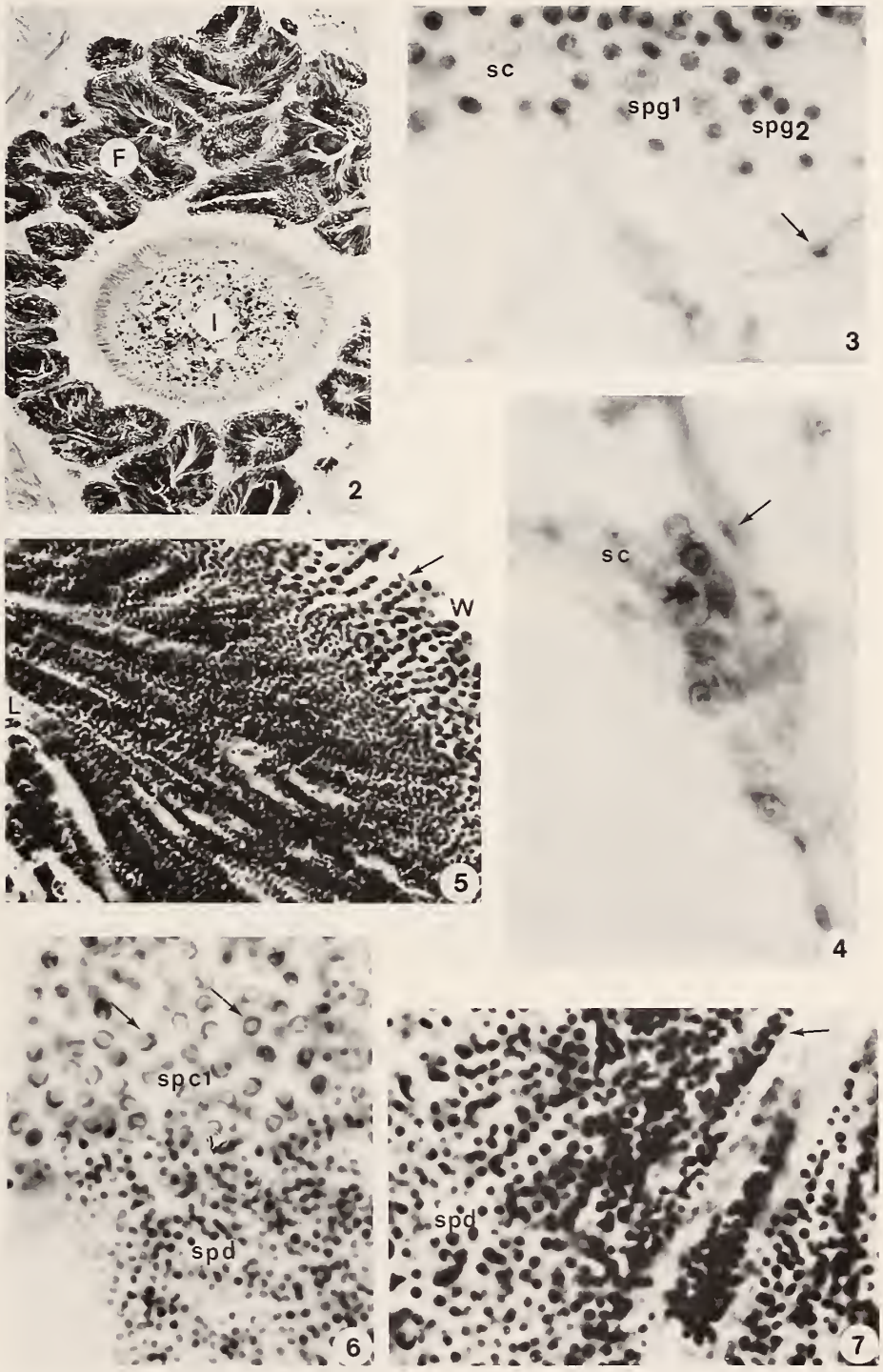
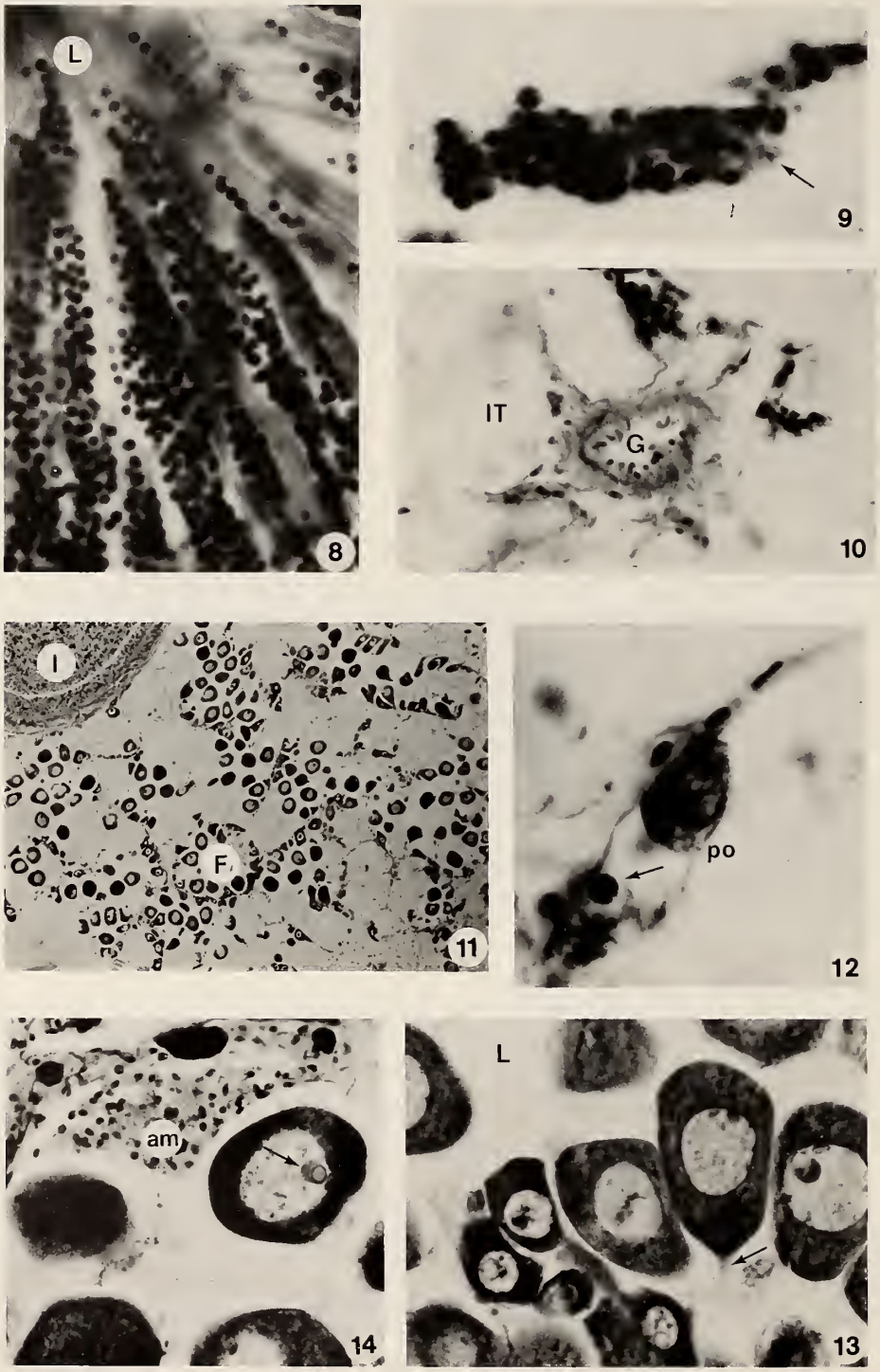


Figure 4. Primary spermatogonia showing some mitotic figures. A spindle-shaped nucleus from a cell of the follicle wall (arrow) is visible and a supporting cell nucleus (sc) is seen next to the germ cells. ×500.

Figure 5. Germ cells within a male gonadal follicle. Primary spermatocytes (arrows) are in single-cell columns oriented from the walls (W) toward the lumen of the follicle (L). ×200.

Figure 6. Primary spermatocytes (spc1) showing meiotic figures (arrows). Next to the primary spermatocytes, a cluster of secondary spermatocytes is interspersed with spermatids (spd). The nuclei of these two cell types are hardly distinguishable. ×500.

Figure 7. Clusters of spermatids (spd). Spermatids in more advanced stages of differentiation (arrow) form radially oriented columns with the flagella oriented toward the center of the follicles. ×500.



Explanation of Figures 8 to 14

Figure 8. Radially oriented columns of spermatozoa and advanced spermatids. Bundles of flagella occupy the lumen (L) of the gonadal follicle. ×500.

Figure 9. Dense mass of amoebocytes within a follicle. The nucleus of a supporting cell (arrow) can be seen. ×500.

Figure 10. A gonoduct (G) in the interstitial tissue (IT). ×200.

Figure 11. Topographical view of the female gonad of *Mesodesma donacium*. The follicles (F) in the visceral mass surround the intestine (I). ×20.

Primary spermatogonia: These spermatogonia have large (about 3 μm diameter) spherical or slightly oval nuclei with scanty and finely granular chromatin and one or more conspicuous nucleoli (Figure 3). Primary spermatogonia are less numerous than secondary spermatogonia and lie against the membrane enveloping the follicles. Occasionally, mitotic figures can be seen in this type of spermatogonia (Figure 4).

Secondary spermatogonia: Spermatogonia of this type have smaller nuclei (2.0–2.5 μm) and stain more heavily than the nuclei of primary spermatogonia. Secondary spermatogonia are more numerous than primary spermatogonia and lie close to them (Figure 3).

Primary spermatocytes: These cells form numerous, compact clusters. They have small nuclei (about 1.8 μm in diameter) that vary in appearance as the chromatin assumes different consistencies and locations within the nucleus. The chromosomes can be scattered in the nucleus or they may be polarized at the periphery, showing typical figures of meiotic prophase (Figure 6).

Secondary spermatocytes: Secondary spermatocytes are seen less commonly than primary spermatocytes. They occur in groups generally intermingled with spermatids, thus forming mixed cell groups. The nuclei of secondary spermatocytes are very similar to those of spermatids (Figure 6).

Spermatids: These cells have small, round nuclei with granular and heavily staining chromatin. They form compact clusters with secondary spermatocytes located toward the center of the follicles (Figure 6). Spermatids in more advanced stages of differentiation form radially oriented columns with the flagella oriented toward the center of the follicles (Figure 7).

Spermatozoa: Spermatozoa are formed in the center of the follicles where they accumulate. The mature spermatozoon has a small round head (1.0 μm in diameter). The chromatin is dense and stains homogeneously. Together with advanced spermatids, mature spermatozoa form columns oriented toward the center of the follicles with bundles of flagella occupying the lumina (Figure 8). Owing to the small size of the sperm head, it is not possible to visualize with the light microscope such structures as the acrosome and middle piece described in the sperm of other bivalves (Retzius, 1904, 1905; Franzén, 1955, 1969, 1983; Ockelmann, 1964; Thompson, 1973; Popham, 1974).

Somatic cells—Supporting cells: These cells have a pale and irregularly shaped nucleus with a prominent nucleolus. The cytoplasm is not visible. Supporting cells are seen next to the follicle walls and intermingled with spermatogonia (Figures 3, 4). Cells of this type are seen in the connective tissue within the follicles when the latter are empty or partially full of gametes.

Amoebocytes: These cells have a nucleus of a size similar to that of the primary spermatocytes, but amoebocyte nuclei are darkly and homogeneously stained and placed toward one edge of the cytoplasm. These cells are especially abundant in follicles that contain residual gametes (Figure 9).

The gonoducts are branched and smaller in diameter than follicles; the walls are lined with ciliated cells, which define a narrow lumen. Gonoducts are seen in the interstitial connective tissue that surrounds the gonadal follicles (Figure 10).

Female Gonad and Germ Cells

As in the male, the female gonad of *Mesodesma donacium* is a branched organ embedded in the visceral mass. Numerous follicles surround the intestinal coils. The follicles are irregular in size and shape, and are delimited by a connective tissue wall (Figure 11).

In the follicles, germ cells at different stages of development can be recognized by their size, shape, and staining properties.

Oogonia: Oogonia are embedded in the follicle walls, frequently in small groups or "nests." The nucleus of an oogonium is spherical, with reticulate and heavily stained chromatin; a nucleolus is not visible (Figure 12). The cytoplasm is scanty or not visible.

Previtellogenic oocytes: The shape of previtellogenic oocytes may be square, oval, triangular, or cylindrical. The scarce cytoplasm is basophilic and bulges from the follicle walls. The nucleus is large, stains lightly, and has disperse chromatin that is usually peripherally placed and prominent; there is a basophilic nucleolus (Figure 12).

Vitellogenic oocytes: The size of vitellogenic oocytes varies with the amount of yolk accumulated. As the oocytes grow they elongate and protrude into the center of the follicles. The basal region of the cytoplasm is thinner than the distal end, forming a stalk that attaches oocytes to the follicle walls. The nucleus is prominent (Figure 13).

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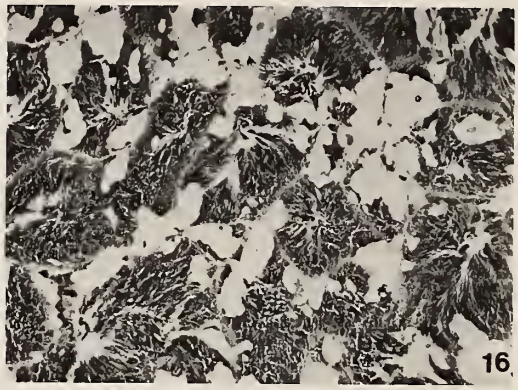
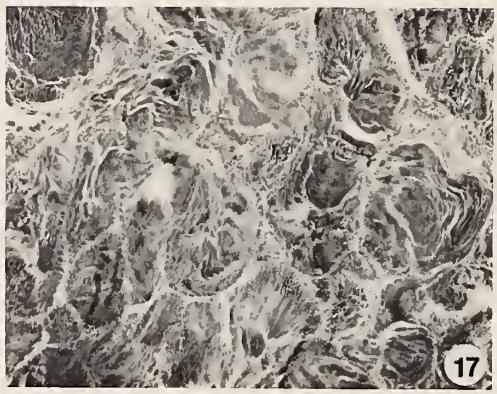
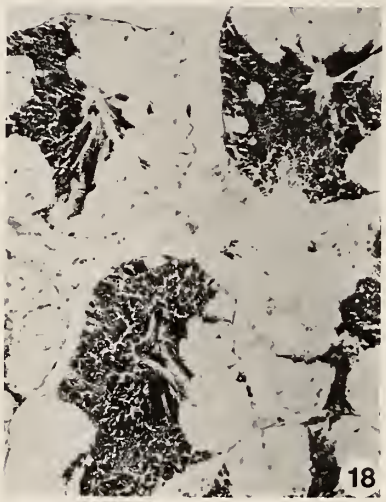
Figure 12. Oogonium (arrow) embedded in the follicle wall. Next to it a previtellogenic oocyte (po) is seen bulging from the follicle wall. ×500.

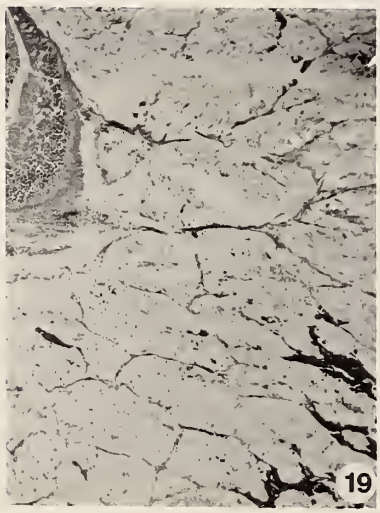
Figure 13. Vitellogenic oocytes of various sizes and shapes protruding into the lumen (L) of the follicle. An oocyte with a slender stalk (arrow) can be seen. ×200.

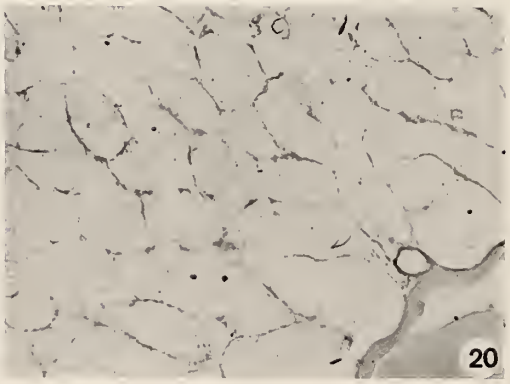
Figure 14. Vitelline (full-grown) oocytes in follicles. The amphinucleolus (arrow) can be seen in one of them. Amoebocytes (am) are seen as dense granular bodies, yellowish in sections. ×200.











Explanation of Figures 15 to 20

Figure 15. Section of gonad tissue from a male *Mesodesma donacium* in the early active stage. Gonadal follicles are small and well delimited. Germinal cells are beginning to invade the intrafollicular spaces.

Figure 16. Section of gonad tissue from a male *M. donacium* in the late active stage. Most of the follicles are almost full of gametes, with small portions of connective tissue remaining. ×20.

Figure 17. Section of gonad tissue from a male *M. donacium* in the ripe stage. Mature sperm form dense masses. Follicles are expanded with their limits poorly delimited. ×20.

Mature oocytes (morphologically mature): Vitelline oocytes are larger than early oocytes and are oval or round. These oocytes have become free of the follicle wall and have moved into the lumen. The germinal vesicle is intact with dispersed chromatin and stains lightly. One or more nucleoli can be seen with eosinophilic and basophilic areas (amphinucleoli). The cytoplasm is loaded with vitelline platelets. The size of mature oocytes ranges from 35 to 48 μm in diameter, with an average of 41 μm (Figure 14).

Somatic cells: Cells similar to the supporting cells of the male follicles can be seen in the female follicles, close to the follicle walls. In the interstitial tissue and in follicles containing residual gametes, one can see amoebocytes having the same features described for those of the male gonad. These cells are frequently seen as dense, yellowish, granular bodies in the female follicles.

Gonadal Cycle

Histological examination of the gonads in *Mesodesma donacium* allows recognition of the following stages of development: early active, late active, ripe, partially spawned, spent, and recovery.

Male gonad—Early active stage: This is a phase of intense gamete proliferation and development. Gonadal follicles are rather small and are clearly demarcated by relatively thick walls. The interstitial tissue is abundant and disseminated among the gonadal follicles. Germinal cells are beginning to invade the intrafollicular spaces (Figure 15). Primary and secondary spermatogonia are close to the thickened follicular walls. Primary spermatocytes proliferate toward the lumina. Occasional spermatids at an initial stage of differentiation can be seen close to primary spermatocytes toward the center of the follicles. Most of the intrafollicular spaces are filled with connective tissue in which supporting cells can be seen. Supporting cells can also be seen close to the follicular walls.

Late active stage: The remaining spermatogenic stages are seen in the late active stage. Primary spermatogonia are now scarce. In contrast, secondary spermatogonia, primary spermatocytes, and spermatids are numerous. Spermatozoa can also be visualized at this stage of gonadal development. The sperm form radially oriented columns with the tails toward the center of the follicles. Germinal cells do not completely fill the follicles; small portions of the follicles contain connective tissue (Figure 16).

Ripe stage: Gonadal follicles are expanded in the ripe phase with their limits poorly defined. Mature sperm form dense masses in the follicles of clams in the ripe stage (Figure 17). Cells in early stages of spermatogenesis are much less numerous at the periphery of follicles than are sperm.

Partially spawned stage: Partially spawned follicles still contain sperm but these are less numerous than in the ripe stage. Spermatids and primary spermatocytes can be seen located toward the periphery of the follicles (Figure 18).

Spent stage: Most of the follicles contain no spermatozoa or very few, and the lumina are empty (Figure 19).

Recovery stage: Gonadal follicles at this stage are empty, except for residual gametes. Close to the follicular walls lie supporting cells and numerous amoebocytes. The interstitial tissue has increased, branching from the intestine and surrounding the follicles (Figure 20).

Female gonad—Early active stage: In the early active stage there is an intense proliferation and growth of gametes. Gonadal follicles are small and well delimited by thickened walls. Interstitial tissue is abundant. Embedded in the follicular walls are oogonia and, bulging to the center of the follicles, previtellogenic oocytes can be seen. Vitellogenic oocytes of different size and shape lie at the periphery of the follicle walls and the cytoplasm extends into the lumen of the follicles (Figure 21).

Late active stage: In the late active phase, vitellogenic oocytes are more numerous than in the early active stage. In addition to vitellogenic oocytes of various sizes, some mature oocytes are free in the lumina of the follicles (Figure 22).

Ripe stage: Ripe gonads typically have a dense appearance because the follicles are crowded together and filled with mature (full-grown) oocytes (Figure 23).

Partially spawned: In partially spawned gonads a few vitelline (mature) oocytes are free in the lumen of the follicles and some vitellogenic oocytes are attached to the walls. Less often, follicles are devoid of ripe oocytes (Figure 24).

Spent stage: In spent gonads most of the follicles are devoid of ripe gametes, with few residual oocytes. Other follicles, less numerous, contain a few full-grown and even vitellogenic oocytes (Figure 25).

Recovery stage: In the recovery stage most of the follicles are completely devoid of gametes, although some follicles have a few residual oocytes. Amoebocytes are present within the follicles, close to the walls and in the center

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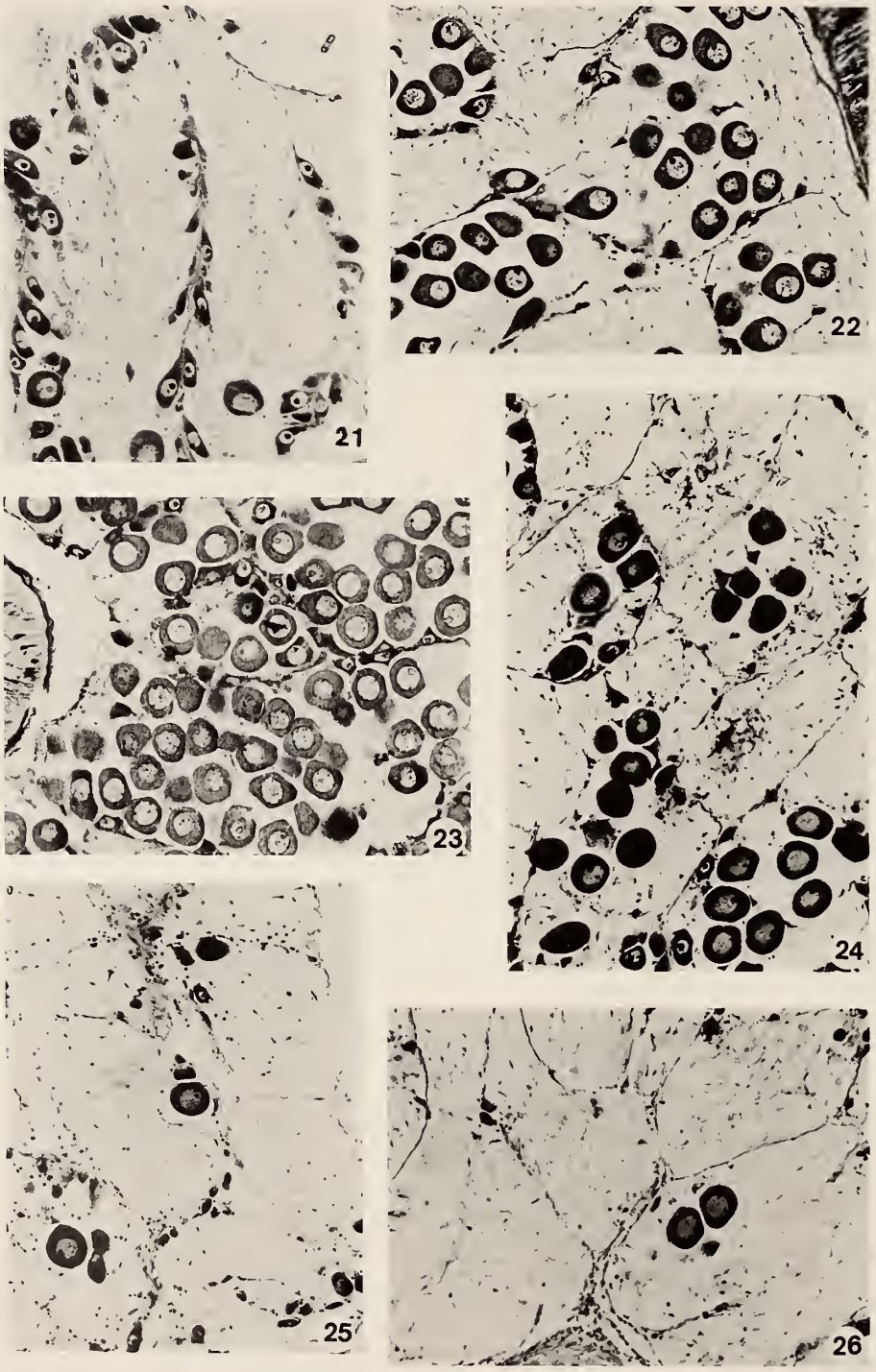
Figure 18. Section of gonad tissue from a male *M. donacium* in the partially spawned stage. Follicles still contain sperm but these are less numerous than in the ripe stage. Spermatids and primary spermatocytes are located toward the periphery of the follicles. ×50.

Figure 19. Section of gonad tissue from a male *M. donacium* in the spent stage. Almost all of the follicles contain no spermatozoa, but a few others still have scarce gametes. ×20.

Figure 20. Section of gonad tissue from a male *M. donacium* in the recovery stage. Follicles are empty except for residual gametes. Interstitial tissue has increased, branching from the intestine and surrounding the follicles. ×20.



Explanation of Figures 21 to 26

Figure 21. Section of gonad tissue from a female *Mesodesma donacium* in the early active stage. Embedded in the follicular walls are oogonia, and vitellogenic oocytes can be seen bulging toward the center of the follicles. ×50.

Figure 22. Section of gonadal tissue from a female *M. donacium* in the late active stage. Vitellogenic oocytes are larger and more numerous than in the former stage of gonad development. Some vitelline oocytes can be seen free in the lumina of the follicles. ×50.

Figure 23. Section of gonad tissue from a female *M. donacium*

Table 1

Percentage frequency of the sampled population of *Mesodesma donacium* from Queule Beach in each reproductive phase during the study period.

	Early active				Late active				Ripe				Partly spawned				Spent			
	Males		Females		Males		Females		Males		Females		Males		Females		Males		Females	
Date	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Sept. 83	0	0	0	0	8	53	12	87	7	47	4	13	0	0	0	0	0	0	0	0
Oct. 83	0	0	0	0	1	8	7	70	12	92	3	30	0	0	0	0	0	0	0	0
Nov. 83	0	0	0	0	0	0	3	19	15	100	13	81	0	0	0	0	0	0	0	0
Dec. 83	0	0	0	0	0	0	0	0	3	24	0	0	10	76	11	100	0	0	0	0
Jan. 84	0	0	0	0	0	0	0	0	1	7	0	0	14	93	15	100	0	0	0	0
Feb. 84	0	0	0	0	0	0	0	0	2	13	0	0	2	13	11	100	11	73	0	0
Mar. 84	0	0	0	0	0	0	0	0	0	0	0	0	6	43	5	33	8	57	10	66
Apr. 84	0	0	0	0	0	0	0	0	0	0	0	0	2	12	3	25	14	88	9	75
May 84	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Jun. 84	16	100	23	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Jul. 84	9	50	18	100	9	50	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aug. 84	0	0	13	86.6	14	80	2	13.4	3	20	0	0	0	0	0	0	0	0	0	0

of the follicles. Interstitial tissue occurs in the spaces between the loosely arranged follicles (Figure 26).

Annual Reproductive Cycle

Histological examination of the gonadal sections revealed a seasonality of gonadal stages (Table 1, Figures 27, 28). During the study period (August 1983–November 1984) male clams in the late active stage were encountered from July to September and females from August through September. In September 1983, 53% of the males and 87% of the females were in this stage. During October, 92% of the males and 30% of the females were in the ripe stage. Ripe males (100%) and females (81%) were most abundant in November.

Clams in a spawning condition were first encountered in December and were last observed in the early April 1984 samples. Males in this stage were most abundant in January (93%) and then declined in the following months (February, March, and April) to 13%, 43%, and 12% respectively. Females in partially spawned stage were most abundant (100%) from December through February and then dropped to 33% and 25% in March and April respectively.

Spent clams were present from February to April, with the highest percentage of males (73%) occurring in February and the highest percentage of spent females (75%) in April. Histological examination of gonads during April revealed that clams in the spent stage had already initiated the resting or recovery stage.

Even though no samples were collected in May 1984, the observed histological features of the gonads in April and in June 1984 suggested that during May, clams were in the recovery stage, a condition observed in part of the population in April.

In June, 100% of the males and females were in the early active stage. During July, 50% of the males were in the early active phase and the other 50% were the first individuals encountered in the late active stage. In the same month (July), 100% of the females were still in the early active phase.

In August 1984, the last month in which samples were histologically examined, 80% of the males and 10% of the females were in the late active stage. This low percentage

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in the ripe stage. The gonad has a dense appearance with follicles crowded together and filled with vitelline (full-grown) oocytes. ×50.

Figure 24. Section of gonad tissue from a female *M. donacium* in the partially spawned stage. Some follicles have a few vitelline and vitellogenic oocytes attached to the walls. Other, less numerous follicles are completely devoid of oocytes. ×50.

Figure 25. Section of gonad tissue from a female *M. donacium* in the spent condition. In this stage, most of the follicles are devoid of gametes, with a few residual oocytes. Other, less numerous follicles contain some full grown and even vitellogenic oocytes. ×50.

Figure 26. Section of gonad tissue from a female *M. donacium* in the recovery stage. Most of the follicles are completely devoid of gametes, but other, less numerous follicles contain residual gametes. Interstitial tissue extends from the intestine wall among the loosely arranged follicles.

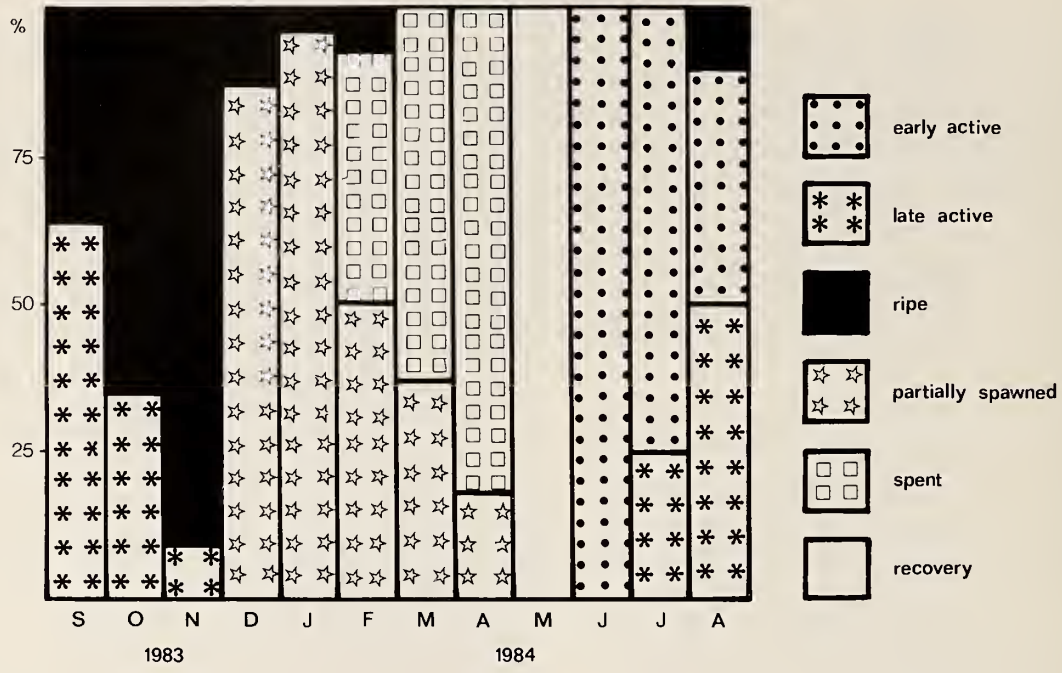

Figure 27

Reproductive cycle of *Mesodesma donacium* from Queule Beach during the study period. The length of each shaded area represents the percentage frequency of the population in each reproductive phase.

shows that August corresponds to the beginning of the late active phase in females. This stage extends through September and October as revealed by the histological examination of gonad sections at the beginning of the study period.

The dry weight of specimens changed throughout the year. A first increase in the dry weight was shown in November–December and then it decreased in January. A second increase in the dry weight of specimens was observed in March, followed by a progressive decrease from that month until the end of the study (Figure 29).

DISCUSSION

Male germ cells recognized in *Mesodesma donacium* correspond to the usual types observed in the spermatogenesis of various marine bivalves (Sastry, 1977), thus indicating that this process in *M. donacium* follows the same general plan described elsewhere in invertebrates as well as in vertebrates (Roosen-Runge, 1977).

Two types of spermatogonia can be recognized (Figure 3). Primary spermatogonia derived from primordial germ cells proliferate and give rise to secondary spermatogonia, which are definitive spermatogonia as these are the end products of spermatogonial mitosis (Figure 4). Secondary spermatogonia directly give rise to primary spermatocytes.

Secondary spermatocytes were difficult to identify. Apparently meiotic division is rapid at this stage; consequently, secondary spermatocytes would be very transient cells, giving rise to spermatids (Giese & Pearse, 1977; Roosen-Runge, 1977). Probably the nuclei of secondary spermatocytes are very similar to those of initial spermatids and thus they cannot be distinguished using light microscopy.

Neither cells of atypical spermatogenesis nor atypical sperm, described in several marine bivalves and gastropods (Loosanoff, 1937a, 1953; Coe & Turner, 1938; Ankel, 1958; Bulnheim, 1962; Nishiwaki, 1964; Ockelmann, 1965; Shaw, 1965), were observed in the spermatogenesis of *Mesodesma donacium,* thus indicating that in this species atypical spermatogenesis does not occur or occurs very rarely.

Somatic cells observed within gonadal follicles in *Mesodesma donacium* correspond to two different functional types of cells. The first and more abundant type corresponds to supporting and, possibly, nutritional cells. Somatic cells of the second type are phagocytic cells (amoebocytes) which are similar to those called cell Type C by Tranter (1958). Phagocytic cells have been described in the gametogenesis of several bivalves. Such cells also have been assigned a nutritional role (Loosanoff, 1937b; Tranter, 1958; Wilson & Hodgkin, 1967).

Oogenesis in *Mesodesma donacium* has the usual characteristics described for other marine bivalves. It was not possible to distinguish primary and secondary oogonia, as described in other mollusks (Tranter, 1958; Raven, 1961). Diffuse chromatin of the nucleus of previtellogenic oocytes indicates that these oocytes are in the vegetative phase

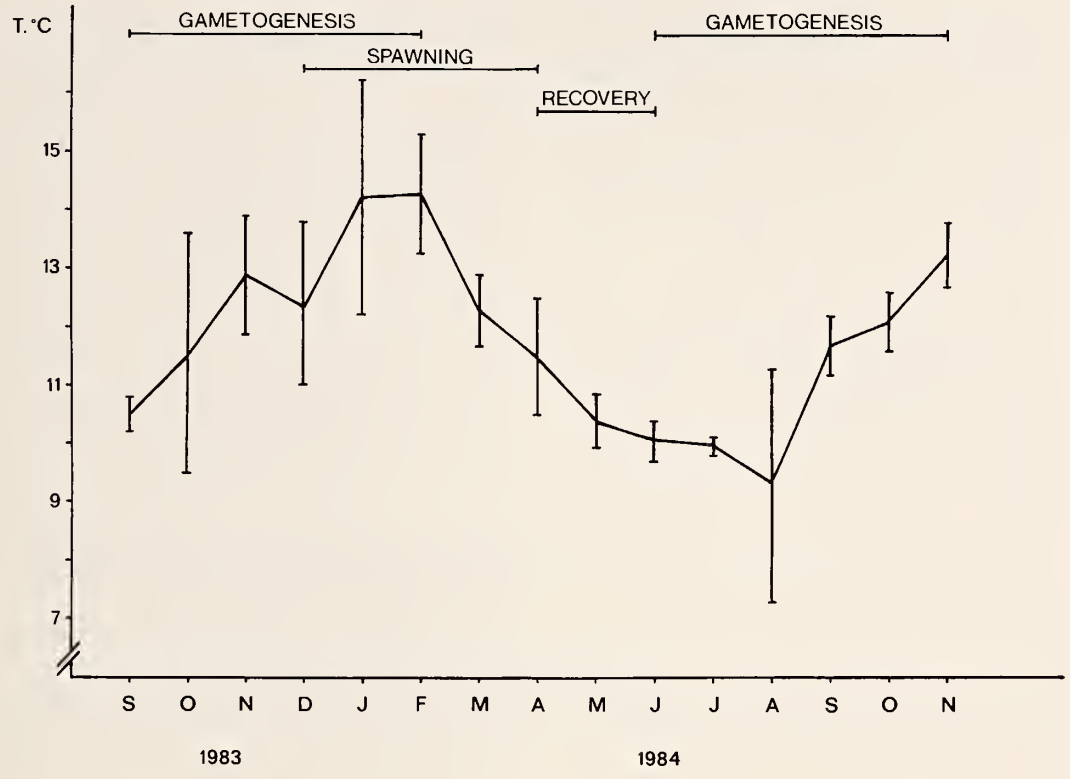

Figure 28

Monthly mean, and standard deviation, of water surface temperature at Mehuín (39°25'S, 73°13'W), located next to Queule Beach, during the study period. Corresponding periods of gametogenesis, spawning, and recovery are indicated for reference.

(Raven, 1966), that is, in meiosis arrested at early prophase.

Growing oocytes with a cytoplasmic stalk have also been described in several marine bivalves (Saleuddin, 1964; Ropes, 1968; Porter, 1974; De Villiers, 1975; Rae, 1978) including Chilean bivalves (Cifuentes, 1975; Lozada & Reyes, 1981; Lozada & Bustos, 1984) and also in freshwater bivalves (Beams & Sekhon, 1966; Zumoff, 1973; Peredo & Parada, 1984). Beams & Sekhon (1966) assign a mechanical and also a possible nutritional role to the cytoplasmic stalk. Mature (full-grown) oocytes show the germinal vesicle intact, thus indicating that meiosis is not completed within the gonadal follicles, a situation also described in other bivalves such as *Crassostrea virginica* (Galstoff, 1937), *Spisula solidissima* (Ropes, 1968) and *Donax serra* (De Villiers, 1975). This situation is turn differs from that in other bivalves such as *Cyprina islandica* and *Venus mercenaria* (Loosanoff, 1953), *V. striatula* (Ansell, 1961), *Mya arenaria* and *Mercenaria mercenaria* (Stickney, 1963), in which at the time of ovulation, the oocytes possess broken down germinal vesicles and the chromosomal spindle is formed. Possibly *Mesodesma donacium* oocytes, like *S. solidissima*, requires fertilization for germinal vesicle breakdown to occur and, consequently, meiosis to be re-initiated (Allen, 1953; Tumboh-Oeri & Koide, 1982). Therefore, in *Mesodesma donacium*, full-grown oocytes contained in gonadal follicles reach only morphological maturity; physiological maturity is achieved once they have left the gonad.

Reproductive Cycle

Histological examination of gonad sections during the study period allowed us to determine that the reproductive cycle of *Mesodesma donacium* is a biological event with annual periodicity. A maturation period occurs from June through November (winter and spring) and a spawning period extends from December to April (summer–early autumn), followed by a short recovery period during May, and then the start of a new cycle.

The percentage of individuals of the population in different stages of gonadal development during the study period (Table 1) indicates that males and females are in synchrony at the beginning of the maturation period (early active stage) because practically 100% of the males and females are in the early active stage during June. This synchrony disappears as the maturation period proceeds (late active and ripe stages), such that during October, 92%

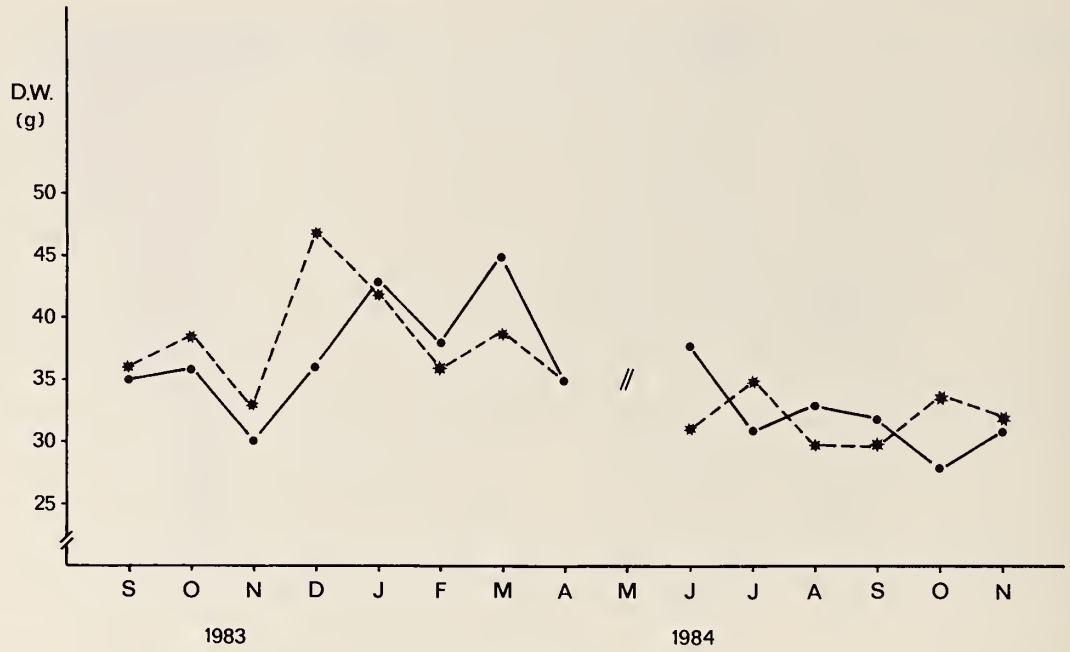

Figure 29

Seasonal changes in soft tissues in *Mesodesma donacium* from Queule Beach, calculated for a standard animal of 70-mm shell length (males —·— and females ---*---).

of the males are in the late active stage, whereas in that month only 30% of the females are in the same stage of gonadal development. In November, 100% of the males and 81% of the females have reached the ripe stage. The differences in the timing of the gonadal condition of the two sexes is attributable to the different rate at which spermatogenesis and oogenesis proceed, the latter being a slower process mainly owing to the accumulation of food reserves in the oocytes.

The spawning period starts in December in both sexes, as no specimens in that condition were registered before then. Spawning is partial and asynchronous. In December, 100% of the females were in the partial spawning stage. In males, the highest proportion of individuals in that condition was observed one month later (January). Even though in males the onset of spawning occurs gradually, this stage ends more abruptly than in females: by April, 88% of the males were in the spent stage whereas only 75% of the females were in that stage in the same month.

Although adverse climatic conditions hampered sampling in May, the histological characteristics of gonads in both sexes in the month immediately before (April, 1984) and immediately after (June, 1984) indicate that during May, gonads are in the recovery phase, a stage already present in a proportion of the individuals examined in April. This indicates an overlap between the spent and recovery stages, the majority of the population being found in the latter stage during May.

Although the percentages of clams in different stages of gonadal development show that the entire population of *Mesodesma donacium* does not reach ripeness at the same time, the majority of the population was ripe at the beginning of the spawning phase. This shows that the breeding period of *M. donacium* in the study area is limited to a certain period of the year (summer–early autumn) coincident in this respect with several bivalves that have an annual reproductive cycle with only one spawning period. A similar situation has been described in *Mercenaria mercenaria* and *Cyprina islandica* (Loosanoff, 1937b, 1953), *Mya arenaria* (Coe & Turner, 1938; Ropes & Stickney, 1965; Porter, 1974), *Venus striatula* (Ansell, 1961) and *Macoma balthica* (Lammens, 1967) among others. The congeneric species *Mesodesma mactroides* that inhabits the Atlantic coast of South America has two breeding periods: October–December and February–March (Olivier *et al.*, 1971).

The results of the present study differ from those reported on the reproductive cycle of populations of *Mesodesma donacium* occurring at other latitudes on the Chilean coastline. Brown & Guerra (1979) reported that the *M. donacium* population in Guanaqueros, northern Chile (30°15′S, 71°40′W) spawns in spring–summer, with the maximal intensity at the beginning of November, followed by a resting period. Tarifeño (1980) determined the maturation period of *M. donacium* at Laguna Beach in the Valparaíso area, central Chile (32°30′S, 71°30′W) to be during the fall–winter season (April through July). There, the maximal population ripeness was reached in mid-win-

ter and the spawning season extended from the end of the winter to the beginning of spring. The resting period of that population extended from spring to mid-autumn (October through May).

The observed differences in the timing of the different phases of the reproductive cycle in *Mesodesma donacium* in the different latitudes are probably ascribable to local variations of environmental factors, the major ones being water temperature and the availability of food. Several authors have reviewed the influence of temperature on the reproductive cycle of marine invertebrates. As an external factor, temperature can exert a selective pressure in the determination of the breeding season of a species (ultimate factor) and its fluctuations act as external clues that synchronize the reproductive cycle of a species (proximate factor) (Giese, 1959; Fretter & Graham, 1964; Giese & Pearse, 1977).

Tarifeño (1980) suggests that the increase in water temperature variation that occurs at the end of the winter could trigger spawning of surf clams at Valparaíso. In the area of the present study, the greatest monthly thermal changes occurred in November 1983 and 1984, with the difference between the monthly maximum and minimum temperature being 1.3°C and 1.1°C respectively. Although the maximal thermal oscillations coincided with the end of the maturation period and the beginning of the spawning season, this factor alone, with its meager change, probably does not trigger spawning of the *Mesodesma donacium* population at Queule Beach. The spawning season observed in the present study also coincides with the period of increasing surface water temperature in the area (Figure 28). Therefore, perhaps spawning of the surf clam population at Queule Beach is due to the combined effect of both variables of water temperature: the increase of water temperature and the increase in the monthly thermal oscillation that occurs from November on.

The increase in the phytoplankton biomass registered in the area from spring to mid-autumn (Toro, 1984) represents a greater food supply for planktotrophic organisms. In this way, the reproductive cycle of *Mesodesma donacium* is timed such that gamete emission, from December on, allows larvae to hatch during the season of the greatest abundance of phytoplankton in the area, a period that lasts from November to May (Toro, 1984).

Seasonal changes in the dry weight of specimens (Figure 29) show that the first increase reaches its maximum at the end of spring (November–December) and then dry weight decreases in January. This change is due to the increase in gonad weight at the end of the maturation period, which is followed by the spawning period. The second increase in the dry weight of specimens reaches its maximum in March, after which a progressive decline in dry weight is observed. These variations may be caused by the accumulation of food reserves during the period of food abundance (weight increase) and then by the depletion of these reserves in the maturation period during the winter–spring seasons.

From the above discussion it can be concluded that *Mesodesma donacium* has evolved a reproductive strategy in which gametes are produced during the winter–spring period, utilizing food reserves stored in the gonad itself or in other body tissues. Furthermore, this strategy increases larval survival through gamete emission during the summer and beginning of fall so that clam larvae find an adequate food supply at the time of hatching.

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